



Factors Contributing to the Spread of Hydrilla in Lakes and Reservoirs

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PURPOSE: This technical note reviews case histories on several lakes and reservoirs throughout the United States that are infested with hydrilla (*Hydrilla verticillata* (L.f.) Royle), to evaluate environmental factors regulating its rate of spread. Environmental factors include water chemistry parameters such as alkalinity, conductivity, pH, chlorophyll a, total nitrogen, dissolved ammonia-nitrogen, total phosphorus and transparency (as measured by Secchi disk depth).

BACKGROUND: Two distinct biotypes of hydrilla, a native of Southeast Asia and Australia, occur in the United States. Dioecious hydrilla was first discovered in Florida in the early 1960's (Pieterse 1981), while monoecious hydrilla was initially found in the Potomac River near Washington, DC, in 1982 (Steward et al. 1984). Monoecious hydrilla has both pistillate and staminate flowers on the same plant, while the dioecious biotype produces pistillate and staminate flowers on separate plants (Spencer and Anderson 1986). Both biotypes demonstrate aggressive growth strategies, in which shoots from established plants rapidly elongate to the surface and form a dense canopy. In addition, localized spreading of hydrilla beds results from stoloniferous growth. Perennation of established beds occurs from stem sections, root crowns, and tubers (Madsen and Smith 1999). Long distance dispersal is accomplished through fragments and turions. Dense hydrilla growth can impede navigation, destroy habitat, degrade water quality, and interfere with recreational usage.

Hydrilla is a native of the warmer regions of Asia and Australia (Langeland 1990, Netherland 1997), with present distribution in the United States as far north as Connecticut (Les et al. 1997) and Washington state (Netherland 1997). Through genetic testing, the Connecticut hydrilla was found to be dioecious, while the Washington state hydrilla was determined to be monoecious. Hydrilla can also be found in the Gulf and Atlantic coast states, Tennessee, and the western states of Arizona and California (Les et al. 1997, Netherland 1997).

Many factors have been implicated as limiting aquatic plant growth (Table 1). Although a proper hierarchy illustrating the significance of these factors is difficult to establish, light is typically considered the most significant single factor limiting both distribution and abundance of submersed plants. However, many factors interact in a complex manner to determine the structure of a given plant community, and the distribution, abundance, and rate of growth or spread of an invasive species within that plant community.

Transparency. Limitation of light in aquatic systems is expressed both in the maximum depth to which all plants may grow, as well as in the different species that may colonize and thrive under differing regimes of light. Light penetration is typically measured with a Secchi disk, although more meaningful and accurate measurements can be made with an underwater quantum sensor (from which light attenuation coefficient estimates are generally made). The more turbid the water, the less light that is transmitted, and the greater the light attenuation. Low transparency may be the

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Table 1
Factors Limiting the Potential Abundance, Distribution, Growth, and Spread of Aquatic Plants

Factor	Cofactor	Reference
Light	Availability	Duarte, Kalff, and Peters 1986; Barko, Hardin, and Matthews 1982
	Transparency	Vant et al. 1986
	Depth	Sheldon and Boylen 1977, Dale 1984
Water Chemistry	Inorganic carbon	Adams, Guilizoni, and Adams 1978; Smart 1990; Smart and Barko 1988
	Plant macro-and micronutrients	Barko 1982, Barko 1983
Sediment Chemistry	Plant macro-and micronutrients	Barko and Smart 1981b, 1986; Carignan and Kalff 1979, 1980; Anderson and Kalff 1986
Sediment Texture and Composition	Organic content, particle size	Barko and Smart 1983; Barko, Adams, and Clesceri 1986
Temperature		Barko and Smart 1981a; Barko, Hardin, and Matthews 1982
Competition		McCreary 1991
Disturbance	Abiotic (e.g., wave action)	Chambers 1987
	Biotic (e.g., herbivory)	Lodge 1991
Stress	Salinity	Twilley and Barko 1990

result of numerous factors, including suspended inorganic solids (e.g., silt or clay particles), phytoplankton growth, or dissolved organic material.

Depth. Limitations to plant growth, related to plant depth, are usually attributed to light attenuation. It had been historically asserted that pressure directly limited plant growth at depth, but this was refuted experimentally (Bodkin, Posulsky, and Dale 1980; Dale 1984). In situations where the maximum depth of plants is not regulated by light availability, cold water temperatures of the hypolimnion typically restrict vascular plant growth (Pip 1989).

Water Chemistry. The two most significant components of water chemistry for plant growth are dissolved inorganic carbon (DIC, dissolved carbon dioxide, carbonate, and other forms) and dissolved macro- or micronutrients. Of these, DIC is the most significant. The availability of carbon to submersed plants limits rates of photosynthesis and growth due to two factors. First, diffusion occurs more than 10,000 times more slowly in water than air, and second, concentrations of dissolved carbon dioxide are substantially lower in water than air (Barko, Adams, and Clesceri 1986). Some plants overcome this limitation by utilizing bicarbonate as a carbon source (Raven 1970, Bowes and Salvucci 1989). Some plant macronutrients, such as potassium, are taken up by submersed plants predominately from the water (Barko 1982). Fortunately, most of these water-available nutrients are readily available in surface waters.

Sediment Chemistry. Like their terrestrial counterparts, most rooted submersed plants derive nitrogen or phosphorus from the sediment (Carignan and Kalff 1979, 1980; Anderson and Kalff 1986). Most commonly, rooted plants are limited by nitrogen availability, and occasionally, by phosphorus; both of which are predominantly taken up from the sediment (Barko and Smart 1981b). Water column phosphorus and nitrogen are generally not important to the growth of rooted submersed plants, other than what is eventually absorbed into the sediment. Other aspects of the sediment; e.g., the texture and composition, are also significant to plant growth. High organic content has been shown to reduce rooted plant growth (Barko and Smart 1983). Sediment particle size distribution and physical properties have significant bearing on nutrient-holding capability and stability as a rooting medium.

Temperature. Temperature is an important factor in regulating the rate of growth (Barko, Hardin, and Matthews 1982; Spencer and Ksander 1991), initiating growth in the spring and inducing dormancy in the fall (Madsen and Adams 1988a, 1988b; Barko and Smart 1981a).

Competition. Competition is an important factor in explaining why one species is present and another is not (McCreary 1991). A clear example of competition at work is the suppression and replacement of submersed native plant communities by nonnative species (Madsen et al. 1991, Madsen 1994). Unfortunately, competition has not been extensively studied in submersed aquatic plants.

Disturbance. Several mechanisms can be included under disturbance, which can be either environmental or biological in origin. Environmental disturbances include wave action, which is the most important disturbance limiting the inshore distribution of submersed aquatic plants (Chambers 1987). In addition to human perturbations, biological disturbances can include herbivory (Lodge 1991), agitation of the bottom for feeding (e.g., common carp (Crivelli 1983)), or fish nesting (e.g., sunfish (Carpenter and McCreary 1985)).

Stress. Stress factors include a wide range of candidates, but the most common example in aquatic environments is probably salinity. Most freshwater plants are severely restricted by even moderate levels of sodium chloride in the water (Twilley and Barko 1990, Haller et al. 1974, Hammer and Heseltine 1988).

Following introduction of hydrilla into an aquatic system, the mechanism for expansion proceeds from establishment to dispersal to colony formation. Each stage of this development can be moderated by the environmental factors found in that specific invaded system. The relationship between plant expansion and an environmental parameter will be a solid curve, with suboptimal conditions of other parameters limiting rates in certain scenarios. Thus, the realized growth and abundance of the invading plant is best described by a Gaussian relationship (Figure 1).

METHODS: Unpublished historical environmental data for lakes containing hydrilla were obtained from Alabama, Florida, Louisiana, Texas, and North Carolina; published data were obtained from Virginia (Table 2). Although hydrilla exists in many aquatic systems throughout the southern and coastal states, historical data were not readily available for most systems. Hectares of hydrilla spread for each year, over successive years, were obtained as available for these lakes and reservoir systems. Exponential expansion rates were calculated using regressions of hectares covered by

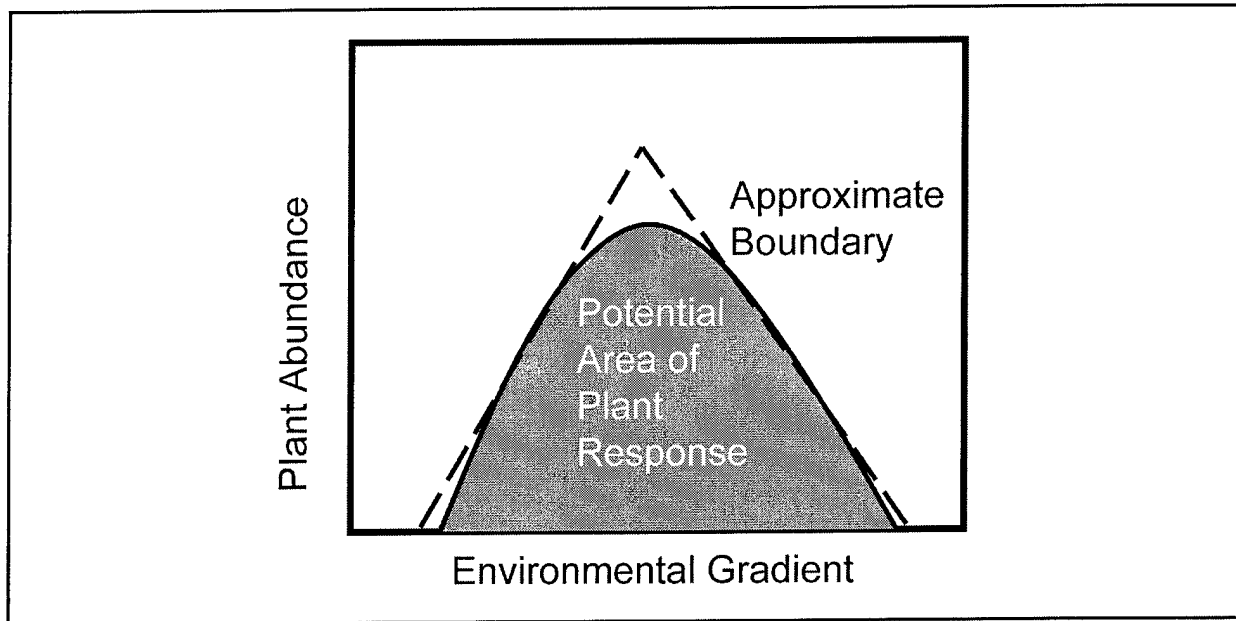


Figure 1. Relationship between plant abundance and an environmental gradient (a similar relationship occurs between the rate of plant spread and an environmental gradient, with suboptimal spread rates occurring during limitation by other environmental factors)

hydrilla over time (Table 3, Figure 2). These expansion rates were then compared to known environmental parameters to determine limits of maximum rates of spread, as concluded by the upper limits of the plot (Madsen 1998).

RESULTS AND DISCUSSION: As indicated above, a wide range of environmental factors work simultaneously to control the distribution and abundance of aquatic plants. These factors may also restrict the rate at which aquatic plants spread within an aquatic system.

Hydrilla exhibits a wide range of temperature tolerance for spread (Figure 3). The large number of points beneath this line of maximum rate of spread may indicate that other factors are regulating the rate of spread, or that the relationship may follow more complicated formulations of growing season or temperature degree-days (Figure 3).

Previous studies have indicated nitrogen as a limiting factor for aquatic plant growth and survival (Smart and Barko 1990). Nitrogen can be found in aquatic systems in different forms, such as ammonia or ammonium, nitrite, nitrate, and total nitrogen (Wetzel 1975). Increased nitrogen in an aquatic system, which can be readily taken up by aquatic plants, promotes a rapid increase in biomass production (Smart and Barko 1990). However, most studies indicate that nitrogen must be present in the sediment for increased concentrations to affect plant growth. In this study, the relationship between calculated rate of spread and ammonia concentration increased initially, and then reached a plateau (Figure 4). This suggests that the actual exponential expansion rate will probably increase until plants experience some saturation level of ammonia, as observed in Michaelis-Menten kinetics, and then further expansion rates will level out due to other factors (Smart and Barko 1990). The response of hydrilla to nitrogen, if any, is most likely due to nitrogen loading that affects both sedimentary and water column nitrogen compartments.

Table 2
Data Sources for Hydrilla Spread and Environmental Conditions in the Reservoir

Lake	State	Hydrilla Data Source	Environmental Data Source
Caddo	TX	3	3
Caney	LA	5	11
Gaston	NC/VA	1, 7	6
Guntersville	AL	10	10
Hatchineaha	FL	9	8
Istokpoga	FL	9	8
Kissimmee	FL	9	8
Lochloosa	FL	9	8
Orange	FL	9	8
Potomac	MD/VA	2	2
Ray Roberts	TX	4	4

1. Mr. Robert Baker, Virginia Power, unpubl. data.
2. Carter et al. 1994.
3. Dr. Roy Darville, East Texas Baptist University, unpubl. data.
4. Dr. Ken Dickson, University of North Texas, unpubl. data.
5. Mr. Charles Dugas, LA Dept. of Wildlife and Fisheries, unpubl. data.
6. Ms. Niki Flint, NC Dept. of Environmental and Natural Resources, unpubl. data.
7. Mr. Robert Gramm, Virginia Power, unpubl. data.
8. Mr. Mark Hoyer, University of Florida, unpubl. data.
9. Ms. Judy Ludlow, FL Dept. of Environmental Protection, unpubl. data.
10. Dr. David Webb, Tennessee Valley Authority, unpubl. data.
11. Mr. Michael Woods, LA Dept. of Wildlife and Fisheries, unpubl. data.

The relationship for calculated exponential expansion rate and total nitrogen initially increased in expansion rate, and then declined with further increases in total nitrogen. The peak occurred at approximately 1.8 mg L⁻¹ total nitrogen (Figure 5). This type of relationship between total nitrogen and expansion rate is similar to that observed for total phosphorus and dominance of Eurasian watermilfoil in Minnesota lakes (Madsen 1998). Water column total nitrogen has not been found to have a direct impact on growth and spread of hydrilla in either laboratory or mesocosm studies. It is more likely that this parameter integrates several factors (e.g., ecosystem fertility for growing macrophytes, growth regulation of macrophytes by light-absorbing phytoplankton populations at elevated fertility (e.g., nitrogen and phosphorus) levels.

Submersed aquatic plants generally obtain phosphorus from the sediments (Barko and Smart 1981b; Bole and Allan 1978; Carignan and Kalff 1979, 1980). Phosphorus is a required macronutrient for aquatic plant growth, but is also important for phytoplankton growth (Carlson 1977, Dillon 1975, Hutchinson 1973, Vollenweider 1968). Elevated concentrations of water column phosphorus can promote algal growth, which will decrease water clarity and inhibit macrophyte growth and survival. Exponential expansion rates may initially increase for hydrilla expansion rates versus water column total phosphorus (Figure 6), then decline; possibly as a result of increased algal growth. Elevated

Table 3
Calculated Spread Rates for Hydrilla in Lake, River, and Reservoir Systems, and Associated Environmental Data

Lake	Bio	Subset	Rate	Temp	Cond	Alk	Secchi	TP	TN	NH ₃	pH	Chl a
Caddo	d	1	2.16	18.42		22.1	75	0.11	2.1	0.48	6.56	
Caney	d	2	2.24	18.42	60.57		171	0.28		0.24	6.7	1.18
	d	1	1.8	18.42	60.57		171	0.28		0.24	6.7	1.18
Gaston	m	1	0.62	15.1	113		157	0.018	0.41	0.016	7.17	9.25
Guntersville	d	1	0.82	16.65	167	60.7	65	0.03		0.04	7.88	14.89
Hatchineha	d	1	0.96	22.2			85.9	0.04	1.2			13.9
	d	2	0.805	22.2			85.9	0.04	1.2			13.9
	d	3	0.33	22.2			85.9	0.04	1.2			13.9
Istokpoga	d	1	0.5	22.3			96.2	0.05	1.1			29.3
	d	2	0.74	22.3			96.2	0.05	1.1			29.3
	d	3	0.59	22.3			96.2	0.05	1.1			29.3
Kissimmee	d	1	1.71	22.2			98.4	0.05	1.2			22.6
	d	2	0.31	22.2			98.4	0.05	1.2			22.6
Lochloosa	d	2	2.57	22.2			58	0.05	1.8			75.1
	d	1	1.39	22.2			58	0.05	1.8			75.1
Orange	d	1	1.07	22.2			94.8	0.04	1.3			37.4
	d	2	1.54	22.2			94.8	0.04	1.3			37.4
Potomac	m	1	0.52	14.3			86	0.04		0.4		15
Ray Roberts	d	1	1.54	18.5	310.2	120.1	65.8	0.18	2.32	0.06	8.03	19.6

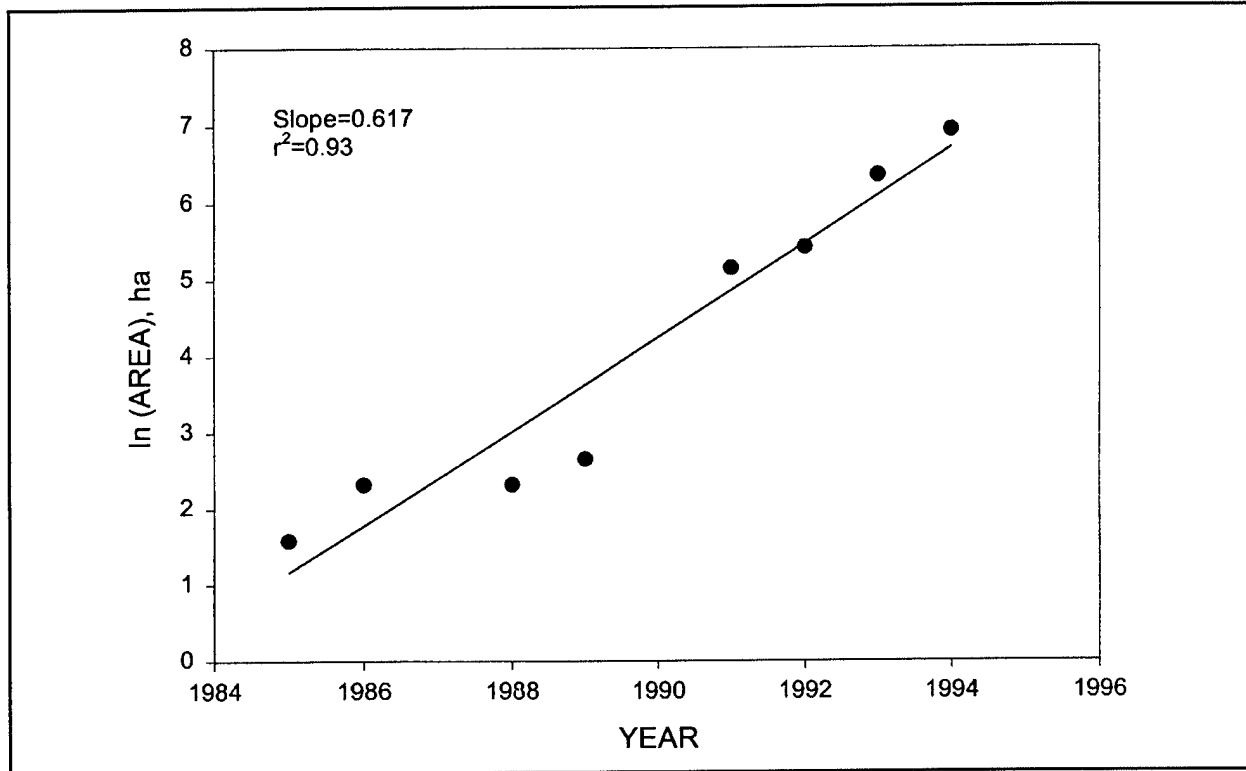


Figure 2. Exponential expansion rate calculated from data on the area of hydrilla versus year, Gaston Lake, NC

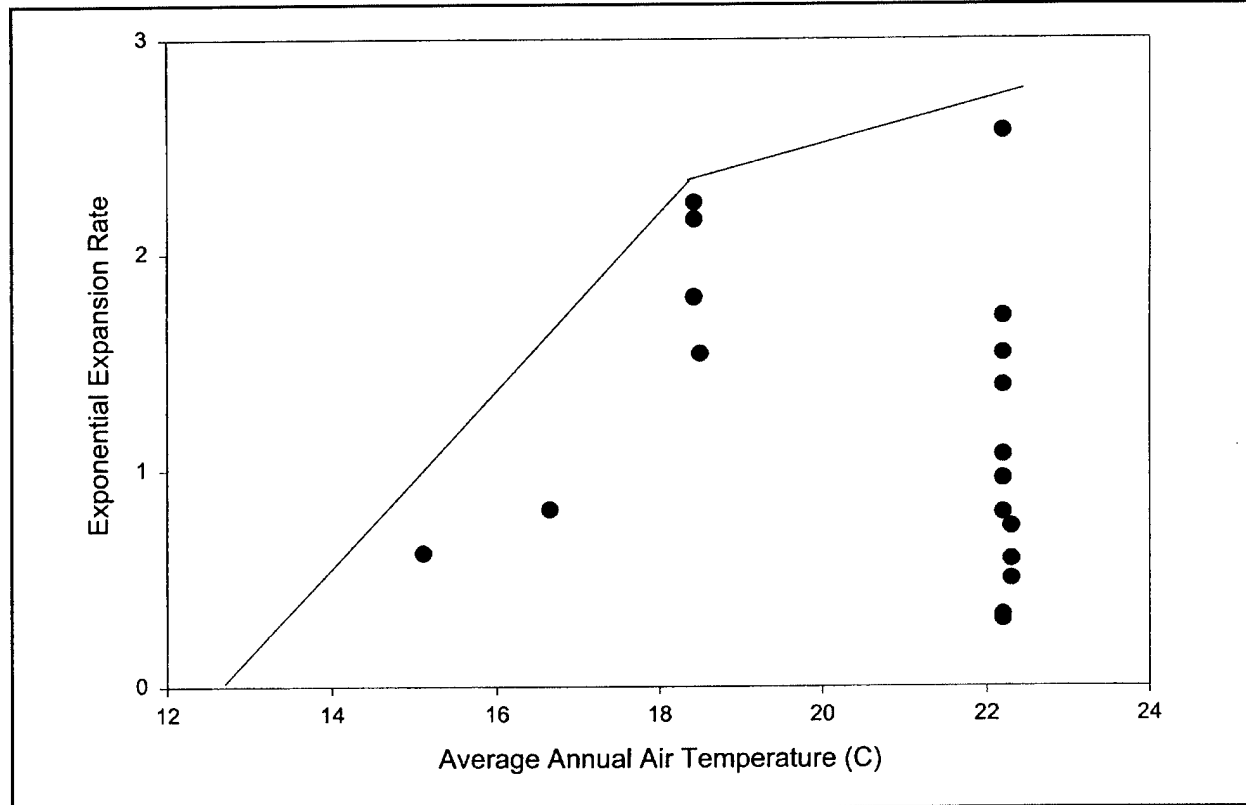


Figure 3. Exponential expansion rate versus annual average air temperature

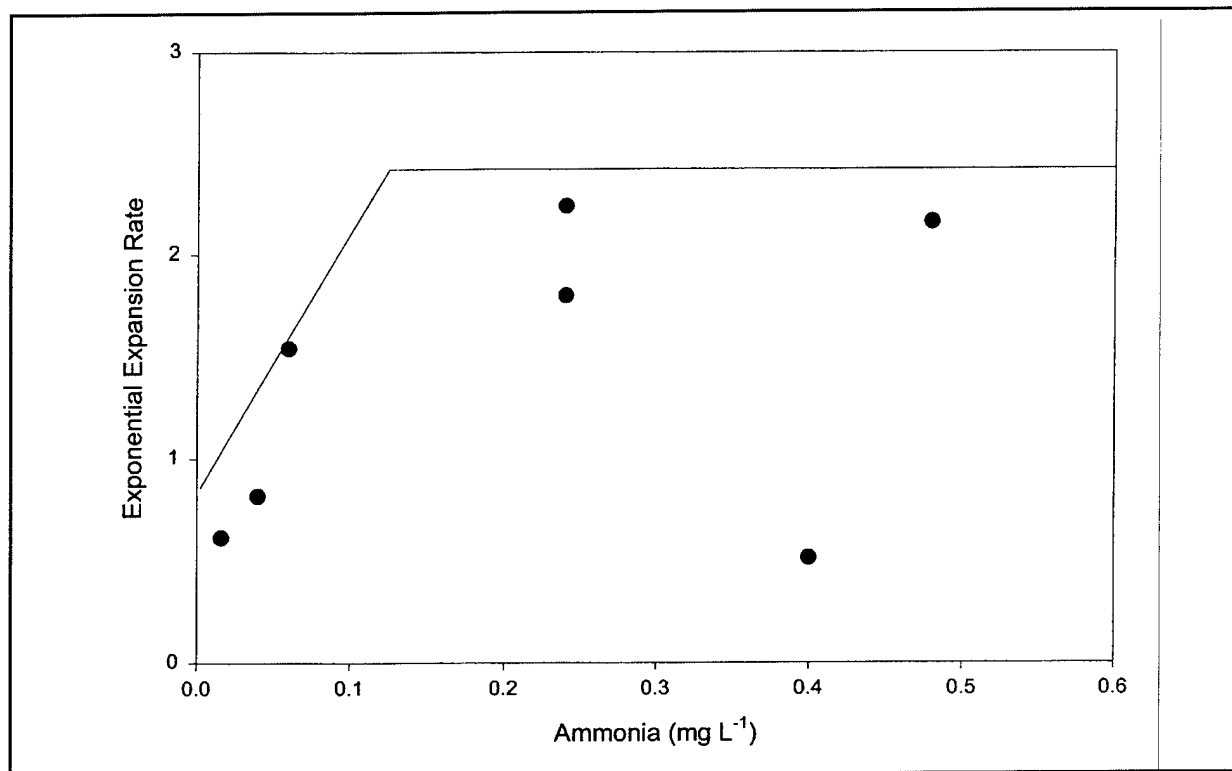


Figure 4. Exponential expansion rate versus total water column free ammonium

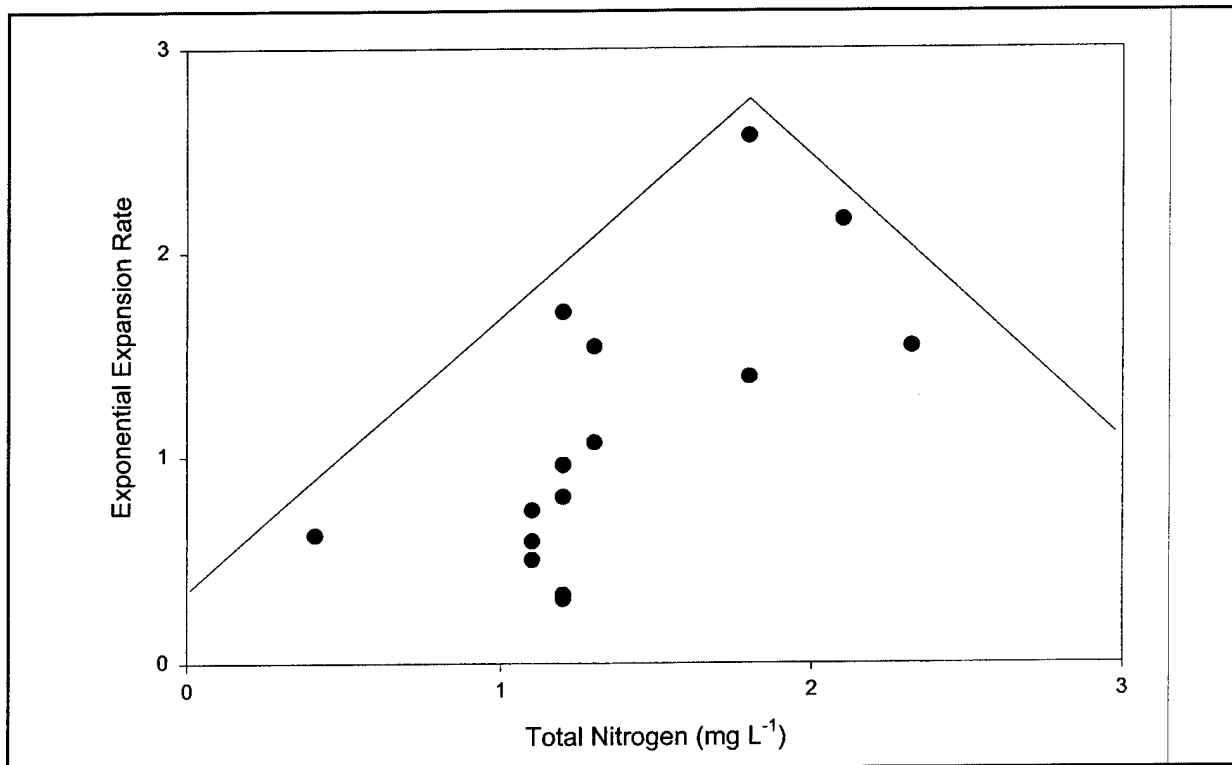


Figure 5. Water column total nitrogen versus exponential expansion rate

chlorophyll a values, which are a measure of transparency and light availability, generally indicate a decrease in exponential expansion rates for hydrilla (Figure 7).

Light is one of the important regulating factors to the growth and spread of plants (Madsen et al. 1996; Pip 1989; Barko, Adams, and Clesceri 1986). Depending on the aquatic system, light limitation can check the ability of hydrilla to spread and survive at increasing depths. However, hydrilla may overcome potential light-limiting conditions by positioning of photosynthetic and meristematic tissues near the surface via stem elongation. This probably accounts for some high expansion rates found in lakes with low Secchi depth values (Figure 8).

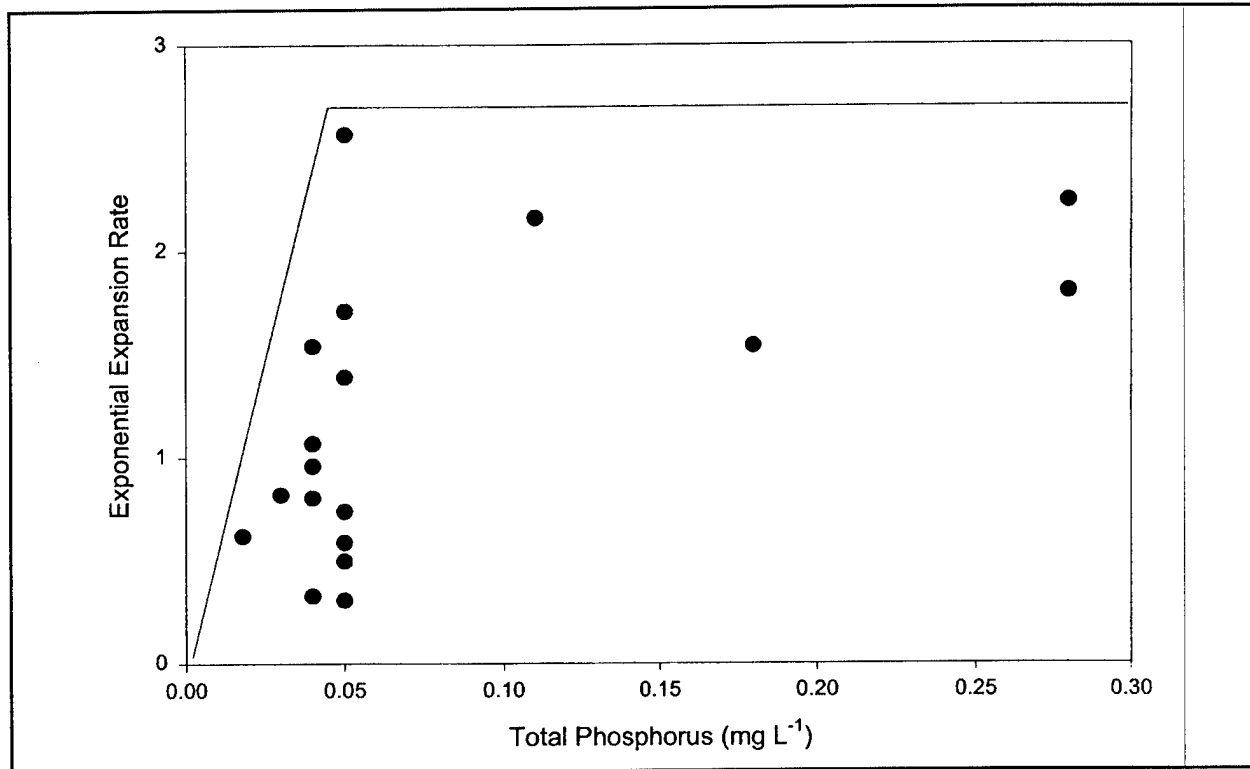


Figure 6. Exponential expansion rate versus water column total phosphorus

Alkalinity represents a measure of the dissolved inorganic carbon available for photosynthesis. Smart (1990) found that growth media with an alkalinity value of approximately 100 mg L⁻¹ provides sufficient dissolved inorganic carbon for the photosynthesis levels necessary for growth and survival of hydrilla. However, reported values for water bodies included in this study were lower than 100 mg L⁻¹. Despite the low alkalinity of these waters, the hydrilla exponential expansion rates ranged from 0.4 to over 2.5 (Figure 9). Hydrilla can adapt to use bicarbonate as a carbon source in photosynthesis (Madsen 1991). The relatively low values here may indicate the bias of data collected for the study, and the general emphasis of studies on hydrilla in the southeastern United States, which tends to have surface waters in the low-to-moderate alkalinity range (Omernik and Powers 1983).

CONCLUSION: The rate of hydrilla spread varies significantly between different water bodies. While the rate of spread should be controlled by environmental factors, no simple linear relationship

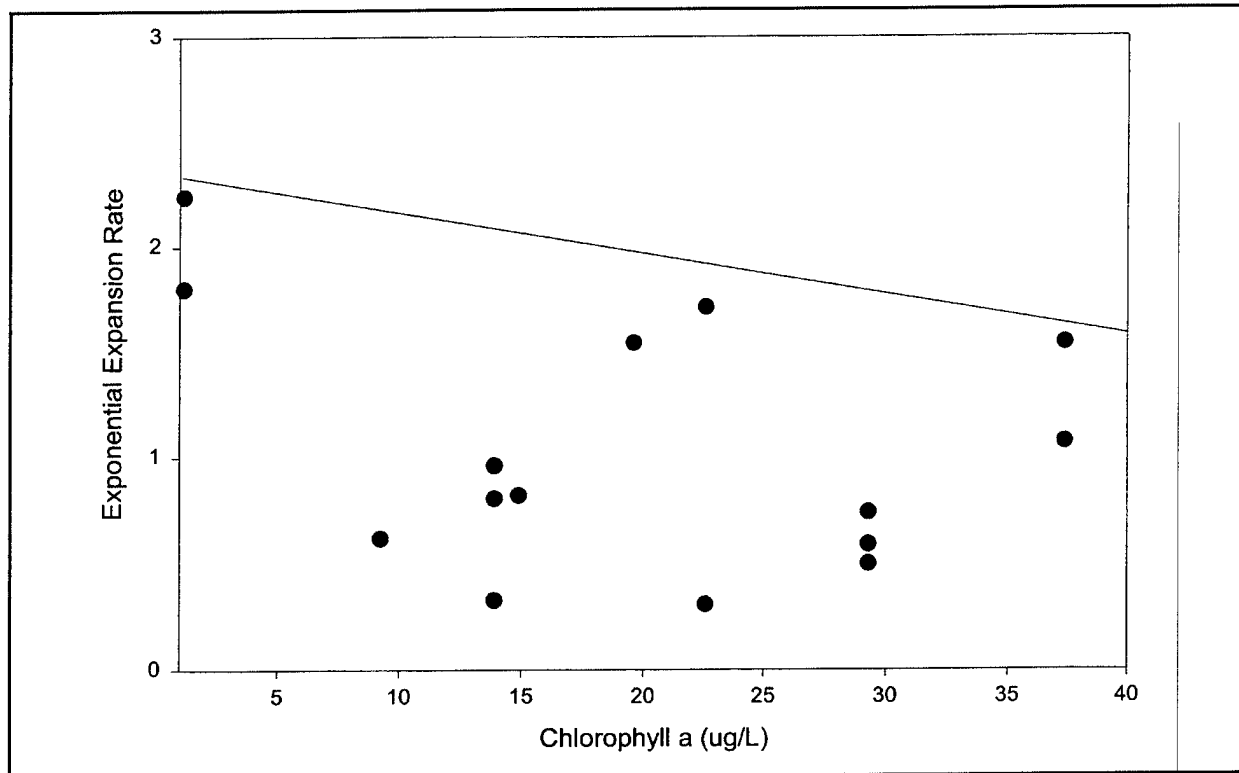


Figure 7. Exponential expansion rate versus water column chlorophyll a ($\mu\text{g L}^{-1}$)

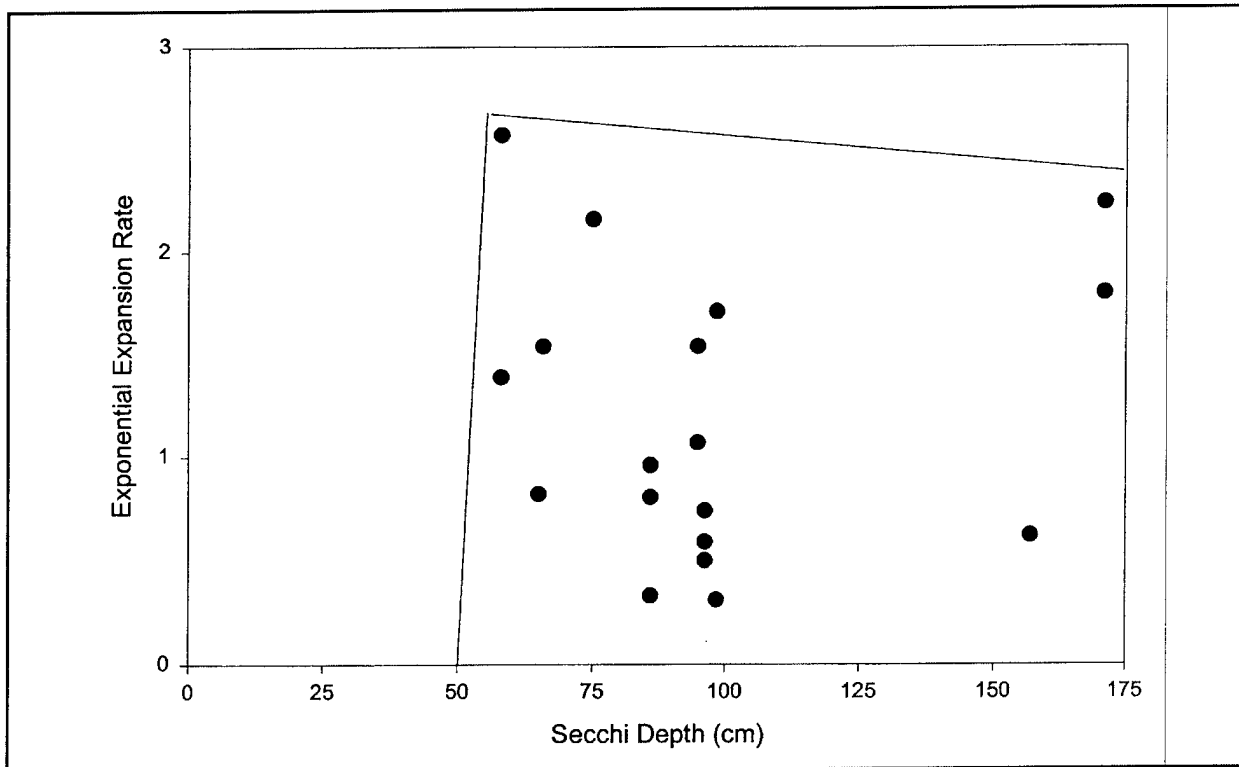


Figure 8. Exponential expansion rate versus transparency, as measured by Secchi disk depth (cm)

was found for factors considered in this study. Rather, the rate of expansion within the studied water bodies was probably controlled by a complex interaction of multiple factors. Factors that appear to be related to hydrilla spread include average temperature, available water-column nutrients, and transparency. Future research will attempt to evaluate the relationships between these factors in greater detail, and attempt to determine which of these factors are most important in regulating the spread of hydrilla in a given lake.

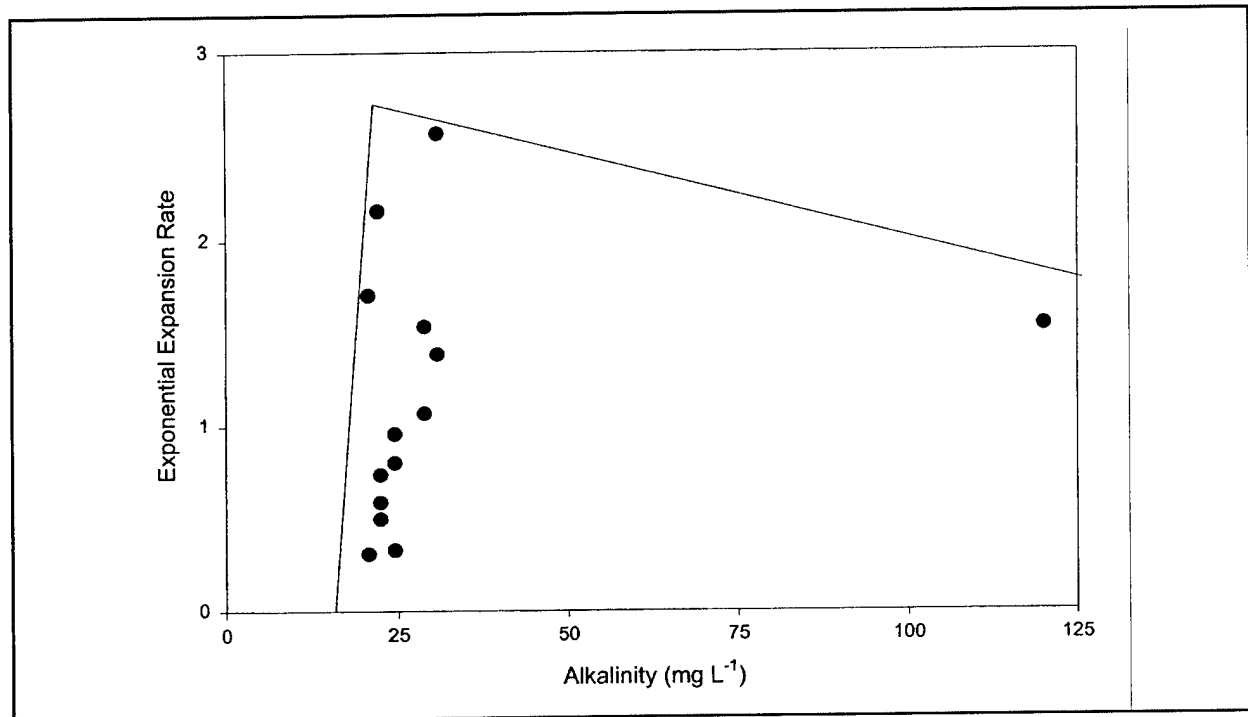


Figure 9. Exponential expansion rate versus alkalinity (mg $\text{CaCO}_3 \text{ L}^{-1}$)

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